

THE SYSTEMATICS OF *CROTAPHYTUS WISLIZENI*,
THE LEOPARD LIZARDS. PART III.
THE LEOPARD LIZARDS OF THE GREAT BASIN
AND ADJOINING AREAS, WITH A DESCRIPTION OF
A NEW SUBSPECIES FROM THE LAHONTAN BASIN

Wilmer W. Tanner¹ and Benjamin H. Banta²

ABSTRACT.—A general analysis of the populations of *Crotaphytus wislizeni* in the Great Basin is presented. A new subspecies, *C. wislizeni maculosus*, for the Lahontan Basin, Nevada, is described and comparisons of color pattern, some scale patterns, and skull measurements are presented.

In Part I of this series we (Tanner and Banta 1963) reported the taxonomic status of *Crotaphytus wislizeni wislizeni* and described the subspecies *C. w. punctatus* from the Upper Colorado River Basin. Part II (Banta and Tanner 1968) dealt with the leopard lizards of Baja California, Mexico, with the description of the subspecies *C. w. neseotes* from Cedros Island. The present study is concerned with the taxonomy of the populations occurring in the Great Basin and adjoining areas west of the Colorado River. With a few exceptions, leopard lizards from this large area have been referred to as *C. w. wislizeni*. However, we note real differences between some populations in this area and those seen from areas to the east (Arizona and eastern Utah), the south (Baja California), and the west (Central California).

The Great Basin is a large geographical area lying between the Rocky Mountains and high plateaus of central Utah on the east and the Sierra Nevada Mountains to the west. Ingress into this area has occurred from the south and southeast with lizards from the southern deserts extending their ranges northward either along the desert ranges or the alluvial valleys. The leopard lizards have used the desert valleys to extend their ranges as far north as southern Oregon and southwestern Idaho.

Specimens from the Great Basin seen by us while preparing the two previous reports were reexamined, and the data are now being added to that pertinent to this report. We have received on loan from Dr. John Wright, Los Angeles County Museum (LACM), a large series of specimens from the southern parts of the Great Basin. These and those seen from other collections (see previous reports) form the basis for this study. Several collections have been made by the authors or their students, in areas not well represented by existing collections, for the purpose of procuring live material. We are grateful to the following for materials sent on loan from critical areas: Mr. James Davis, Indio, California; Dr. Steven C. Anderson, Pyramid Lake, Nevada; Dr. Nathan M. Smith, southern Idaho and southern California; and Mr. M. L. Abts, south central Oregon. Specimens from the Nevada Test Site were obtained by the senior author as a part of the Atomic Energy Commission Grant AT (11-1)-819. Other colleagues and students have aided in the field work and have provided data and suggestions for which we are most appreciative. We are grateful to Drs. Robert C. Stebbins and David Wake for the privilege of examining the extensive collections at the University of California at Berkeley (MVZ), and to Dr. Alan E. Leviton for the opportu-

¹Life Sciences Museum, Brigham Young University, Provo, Utah 84602.

²421 Santa Helena, Solana Beach, California 92075.

nity to examine or receive on loan specimens from the California Academy of Sciences (CAS). We are also grateful for the privilege of studying specimens from the Field Museum of Natural History (FMNH), University of Michigan (UM), University of Kansas (KU), and the U.S. National Museum (USNM).

Perhaps the first report dealing with the leopard lizards of the Great Basin was the notes of C. Hart Merriam (Stejneger 1893), which include observations of these lizards from southwestern Utah, southern Nevada, and east, central, and southern California. Since the report by Stejneger (1893), many articles have referred to the leopard lizards of the Great Basin. However, in none of these is there any change in the taxonomy, since all references refer to *Crotaphytus wislizeni*.

Aside from our previous reports (parts I and II) most other studies have included the leopard lizard as a part of a distribution list or as a part of ecological or natural history notes (Taylor 1912, Richardson 1915, Van Denburgh 1922, Knowlton et al. 1934, 1936, 1946, Allred, Beck, and Jorgensen 1963, Banta 1963, Jorgensen and Tanner 1963, Stebbins 1966, Fitch 1970). Montanucci (1970) analyzed the relationship between the leopard lizards of the central valley of California (*C. w. silus*) and those adjoining populations (*C. w. wislizeni*) in northern Los Angeles and eastern Kern counties, California. In this report on this species we will discuss and characterize those populations occurring in the Great Basin and attempt to indicate the zones of intergradation, as well as the presumed lanes of migration into the present area of distribution.

Those populations in southern California (Imperial, Riverside, and San Bernardino counties) include individuals with varying expressions of the color pattern seen in *C. w. wislizeni* in Arizona and New Mexico. There is a strong tendency for the spots to be smaller and for the rings of white spots to be reduced or absent so that in some large females the pattern is greatly faded and the spots reduced in size and number. In adjacent northeastern Baja California the

few specimens seen are similar and do not indicate any influence from *C. w. copei*. However, those examined from western Sonora (Kino Bay) have dorsal patterns as typical for *C. w. wislizeni* as those from south central Arizona.

In southern and eastern Nevada the trend is toward smaller spots. This also occurs in southwestern Utah, where many individuals are patterned similar to *C. w. punctatus* of eastern Utah. There is a reduction in the numbers of postmentals from southeastern Utah to southwestern Utah and adjoining eastern Nevada. This same pattern exists in much of east central Nevada and the Great Basin of western Utah.

An explanation of the lanes of dispersion used in reaching this large area and the taxonomic explanation of the population diversities are not clear. If we assume that the species had its origin in the desert plateaus of central or north central Mexico, then the following may be an initial attempt at an explanation of what we now see: at the close of the last thrust of the Pleistocene ice age the distribution of *Crotaphytus wislizeni* must have been restricted primarily to the drier, warmer areas of northern Mexico and perhaps some adjoining areas of the southwestern United States. We have no evidence that the leopard lizard populations now extant were isolated as a result of the several ice flow advances or extensive pluvial lake formations. Because of their general morphological similarity and the zones of intergradation occurring between populations, we consider the present distribution of this species to have been established since the Pleistocene.

As the areas to the north and west warmed and dried, these lizards dispersed into the desert valleys formed between the mountain ranges south of the high plateaus in central Arizona and western New Mexico. The first range extensions into this area must have been into the lower valleys extending westward to the Colorado River and northward into the Rio Grande Valley. As the warming trend continued, higher elevations and the more northern areas became occupied. Perhaps at this time the range was rapidly extended up the Rio Grande Valley in New

Mexico, and thus onto the plateaus of New Mexico, Arizona, western Colorado, and Utah. By entering such areas through low areas in the terrain, some populations were removed by distance and partially isolated from the main body of the species. This reduced gene flow and the new and different habitat resulted in adaptive changes in some of the fringe populations, which we now recognize as sufficiently distinct to warrant subspecies designation.

Two basic color patterns exist east of the Colorado River and in northwestern Mexico. Those populations in the low valleys north and south of the U.S.-Mexican border are *C. w. wislizeni*, and those in the high plateaus (mostly upper Colorado River drainage north and east of Grand Canyon) are *C. w. punctatus*. The northeastern population of *C. w. punctatus* has reduced pigmentation on the dorsum; small, widely dispersed spots;

narrow, light cross bands; and an increase in the number of postmentals. If one travels south from the San Juan River of Utah into Arizona and New Mexico the characteristics are modified by an enlargement of the spots and a decrease in the number of postmentals. The zone of intergradation between *C. w. wislizeni* and *C. w. punctatus* is wide, and no attempt is made to define its precise limits. The dorsal spots do increase in size from southeastern Utah across the plateaus south and east into Arizona and New Mexico. In spite of the steep canyons and swift rivers in the Upper Colorado Basin, these leopard lizards have succeeded in crossing them and are established on the west side of the Colorado and Green Rivers in Utah and northern Arizona. From this position they have moved westward from the Colorado River through the gap between the Kaibab Plateau to the south and

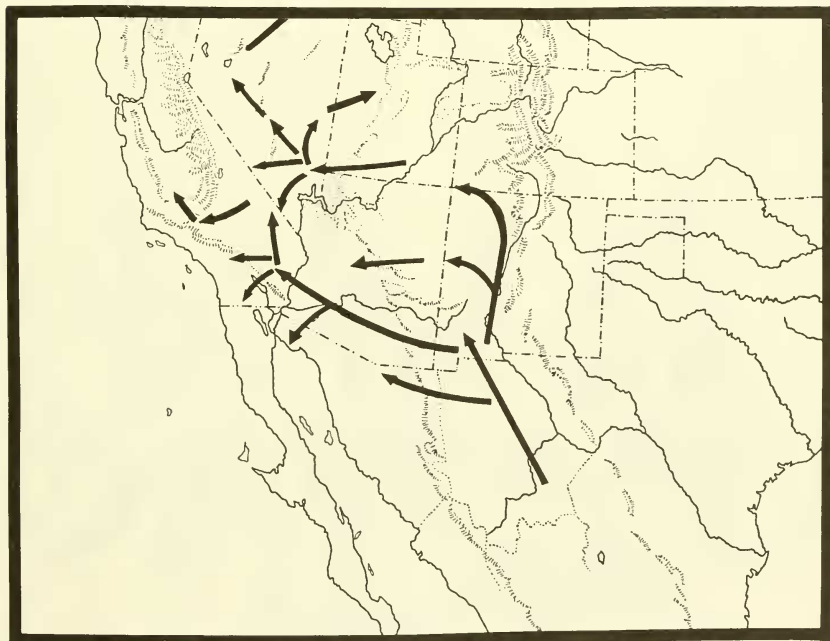


Fig. 1. Possible routes of leopard lizard movement from the ancestral stock to their present distribution since the Pleistocene.

the Paunsaugunt Plateau to the north, to reach the Virgin River drainage in southwestern Utah and southeastern Nevada.

If the above hypotheses are correct, the Great Basin was invaded by leopard lizards originally derived from two populations: 1) Those moving westward through the desert valleys of southern Arizona which crossed the Colorado River, entered southern California, and extended their range south into Baja California Norte and west and north into the Great Basin. 2) Those moving west in southern Utah entered Nevada, where they also expanded south, west, and north into the Great Basin (Fig. 1).

An examination of the populations now extant in southwestern Utah, southeastern Nevada, and southern California show a wide zone of intergradation between these two basic population types (*C. w. wislizeni* and *C. w. punctatus*). A large series from the Nevada Test Site (Mercury, Frenchman, Jackass, and Yucca valleys) contains examples of both of the subspecies indicated above and many color patterns intermediate between them (Fig. 2). The populations in southern Nevada apparently represent a ma-

ajor area of intergradation. As one samples populations to the north and east into extreme eastern Nevada and the Great Basin of Utah, the characteristics of *C. w. punctatus* are strongly evident but with an occasional representative of *C. w. wislizeni* pattern and individuals with intermediate characteristics. To the south particularly, and southwest of the Nevada Test Site, individuals with *C. w. wislizeni* characteristics are seen more often. We are also impressed with the general differentiations in these populations brought about perhaps not only by introgression (hybridization) but also by the natural selection processes. Although most of the valleys in the Great Basin are interconnected either through low passes in the mountain chains or are connected at one or both ends of the discontinuous ranges, there are factors which bring about varying degrees of isolation. In some valleys the effects of isolation and thus some differentiating characteristics are more apparent. This is most obvious in the fringe areas such as the Lahontan and Humboldt valleys in northwestern Nevada, the adjoining areas in northeastern California, southern Oregon,

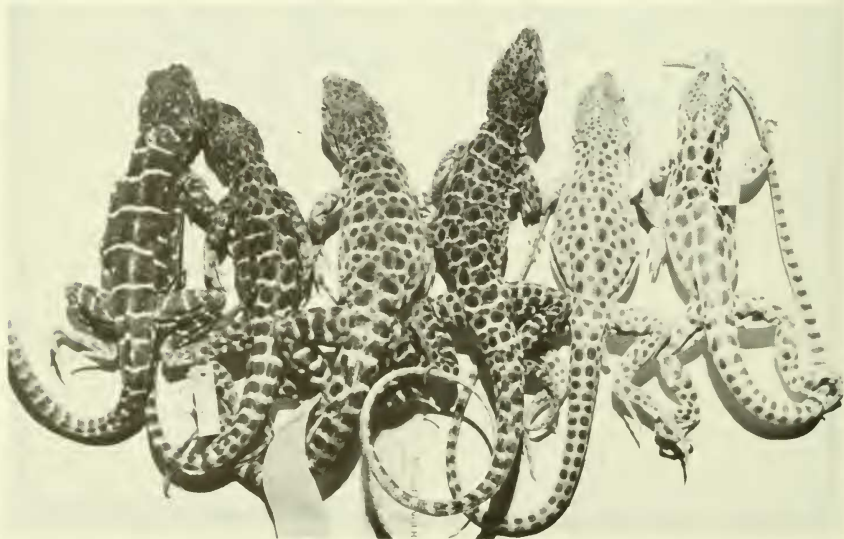


Fig. 2. Individuals showing color pattern variations.

and the Snake River Valley of southwestern Idaho. The population in Antelope Valley (Los Angeles County) also shows some distinct color pattern characteristics which seem to represent some degree of intergradation with the *C. w. silus* population in the San Joaquin Valley.

Montanucci (1970) contends that there is sufficient differentiation between *silus* and the adjoining populations to the south and east to justify full species rank for *silus*. He found that the skull in the *silus* population was shorter than for other *C. wislizeni* populations, and the color pattern is distinct. Furthermore, few intergrades were found nor were there recognizable areas of overlapping for the populations in question.

We have examined a large series of specimens from the south end of the San Joaquin Valley as well as available specimens from along the Tehachapi Mountains from Mojave, both north and south. West from Lancaster and Palmdale, Antelope Valley slowly rises in elevation and narrows as it approaches Frazier Park (at about 3,500 feet) just north of Tejon Pass. On the basis of specimens seen from Antelope Valley, Frazier Park, Grapevine Canyon, and to the west and north of Wheeler Ridge, there is apparently a narrow route into the south end of the San Joaquin Valley. Furthermore, at Frazier Park we find intergrades (CAS 12787-8 and 1243). In northeast Kern County a specimen (CAS 93427) from 1.3 mi W of Cane Wells (7 mi SE of Weldon) has a color pattern very similar to individuals from Washoe County, Nevada. There are other low passes along the Tehachapi Mountains through which entrance into the San Joaquin Valley may have occurred.

We agree with Montanucci (1970) that intergrades are not common between *C. w. silus* in the Central Valley and those populations of *wislizeni* to the south and east. This does not suggest, however, that the two populations will not produce fertile offspring in nature or (and) that the adaptive changes in the color pattern and length of the skull are entirely the result of a gene flow so reduced as to produce reproductive isolation. There is no question that the population in the San Joaquin Valley, once es-

tablished, received only a limited gene flow from the adjacent populations. The nature of the terrain was apparently the principal factor responsible for this reduction, although in recent years human activities south and east of Bakersfield, Kern County, have so altered the habitat that this lizard no longer occurs in wide areas. By eliminating leopard lizards from the areas between the Tehachapi Mountains and Bakersfield, that portion of the population in the San Joaquin Valley most likely to show intergrading characters was also eliminated. There appears to be only one possible area in which there might still be contact between the two populations. That area is from the west end of Antelope Valley, then along the foothills westward to the Pleito Hills and Wheeler Ridge. Even this contact may have been seriously disrupted or closed by recent highway construction.

The entire area extending westward from southern Nevada serves as a potential route of dispersion toward the low passes from the Mojave Desert and into the southeastern end of the San Joaquin Valley of California. This route leads directly into Antelope Valley and the areas south and east of Bakersfield. Extensive agriculture in the south end of the valley has effectively established an artificial barrier between these populations. All of this is, however, very recent, certainly within the last century. There is no reason to suspect that noticeable genetic changes in these populations have occurred in the time since man intervened.

It should be noted that Montanucci (1970) reported some overlap of the skull character between *silus* and other populations of *wislizeni*. Smith and Tanner (1974) found that the collared lizards in the Great Basin (*C. collaris bicinctares*) also was distinguishable from other *C. collaris* subspecies on the basis of cranial anatomy (ratio of width to length). Similarly, we must recognize the possibility that there is proportional variation in the length and width of the skull in the genus *Crotaphytus*. Furthermore, we question the validity of species/subspecies based on the estimated amount of gene flow between populations. If this is important (and we agree that it

plays a role in such deliberations), then what should be done with the numerous insular subspecies in Baja California where gene flow is nil or absent?

We have weighed the pros and cons of species vs. subspecies in this case and can recognize strengths in both alternatives. The occurrence of recognizable intergrades reported by Montanucci (1970) and among the specimens we have seen (even though the intergrades in each study are few in number) is a strong deterrent to the recognition of *silus* as a species. Furthermore, what is to be gained by splitting? We are persuaded, as was Simpson (1945), that such splitting may tend to destroy or dim the true relationship between these populations rather than to establish the basic position of each to each other. We, therefore, retain the leopard lizards in the San Joaquin Valley of California as a subspecies of *Crotaphytus wislizeni* until sufficient data become available to justify the elevation of *silus* to full species status.

The populations in the Great Basin exhibit considerable variation if one examines material from the Salton Sea Basin north into the Lahontan Basin of northwestern Nevada. There are, in fact, two populations with rather distinct color patterns. Those seen from the Coachella Valley south have a faded pattern. This is particularly true for adult females, in which some have few or no spots or bars. In males the pattern is more evident and often reflects traces of the pattern seen in Arizona specimens. Obviously a distinct pattern has not been established, and what we are seeing should be considered, for the present at least, as a developing pattern resulting from adaptive change in the new habitat resulting from partial isolation, but with some influence from the populations to the north and east.

The color pattern throughout a wide area in parts of northern and eastern Riverside County, most of San Bernardino County, eastern Inyo County, California; and in southern Nevada is extremely variable. Nearly all of the color patterns seen in this species have been observed in specimens from the Nevada Test Site, except for the typical *silus* pattern. This wide area of vari-

ability is apparently maintained by continuous gene flow from the northeast (*C. w. punctatus*) and from the southeast (*C. w. wislizeni*). The phenotypes in Fig. 2 are indicative of a large and varied gene pool, which under selective environmental conditions has the potential to produce a wide variety of color patterns.

In contrast to the south and central parts of the Great Basin, the north and western areas comprising the Lahontan Basin and the Snake River Basin from Ada County south and east to at least Bannock County, Idaho, have evolved a distinct color pattern. The most striking variation is in the size and shape of the spots. Because of the large distinct spots, we propose it be known as:

Crotaphytus wislizeni maculosus,
subsp.
Figs. 3, 4d

HOLOTYPE.—An adult male, BYU 32685, taken approximately 200 m W of the lookout point along Nevada Highway 33, west side of Pyramid Lake, Washoe County, Ne-

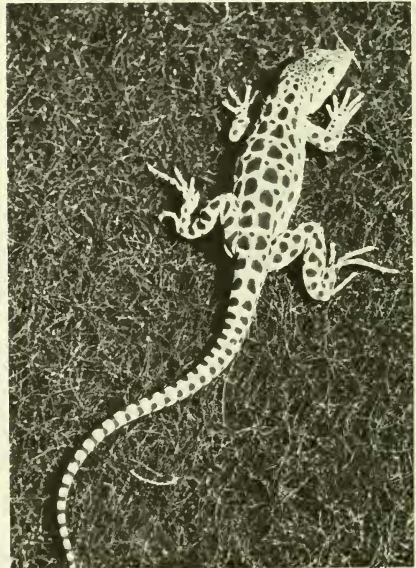


Fig. 3. Dorsal view of the holotype of *Crotaphytus w. maculosus*. BYU 32685, taken on the west side of Pyramid Lake, 24 July 1970.

vada, by Wilmer W. Tanner, on 24 July 1970.

PARATYPES.—Nevada: Washoe County: Topotypes (BYU 32686-7); Pyramid Lake, near south end (BYU 36405-8); Pyramid Lake (CAS 40507-9, 40516-26, 40533-5, and 44157). Idaho: Owyhee Co.: 17 mi SW Nampa, Hwy 78 (BYU 40676-7, 40773, 40815), 14 mi S. Bruneau (BYU 32706); Gooding County: 5.5 mi S. Gooding (BYU 32699-701), 5 mi N. Wendell (BYU 32697-8 and 32704-5); Ada Co.: Foothills N. Boise (SDNHM 1450-2, 23636 and CAS 45426-27, 53775-80).

DIAGNOSIS.—A subspecies of *Crotaphytus wislizeni* most closely related to *C. w. punctatus* and *C. w. wislizeni* to the south and east of its distribution. Distinguished from *C. w. punctatus* and *C. w. wislizeni* in that the dorsal spots are greatly enlarged in size and often quadrangular rather than round. *C. w. maculosus* is distinct from *C. w. punctatus* in having fewer postmentals and greatly enlarged spots and from *C. w. wislizeni* in that there is not a circle of white dots around the larger dorsal spots. In contrast to *C. w. silus* the enlarged dorsal spots are distinct on each side of the middorsal line and between the transverse bars. Individuals have not been seen with the entire dorsal area between the bars pigmented as in most *C. w. silus*.

DESCRIPTION OF TYPE.—An adult male, snout to vent 94 mm, total length 283 mm, tail total length ratio 1.49; dorsal scales (occipital to base of tail) 187; ventrals 93, noticeably larger than laterals and dorsals; scales around middle of body 162, middorsal rows not noticeably enlarged, beadlike; supralabials 16-17; infralabials 16-18; femoral pores 19-20, 2 or 3 small scales on posterior margin of pore; 20 scales between femoral pore series; head scales from rostral to occiput 22, smooth, occiput largest dorsal head scale, but with row of 8 enlarged scales from rostral posteriorly; postmentals 2-2; scales on anterior two-thirds of tail smooth, posterior scales weakly keeled. Head scales smooth, platelike, some raised medially, none imbricate; gulars enlarged near labials, smaller medially, and slightly longer than wide; gular fold prominent;

scales posterior to fold enlarged and these in about 40 longitudinal rows.

Head distinct, 22 mm long, 16.5 mm wide; rostral to ear 22 mm; body slightly flattened, wider than high; longest toe 20 mm. Color pattern consisting of a series of six rows of large dark brown spots extending from head and shoulders to base of tail, middorsal rows and one lateral row extending onto tail; a series of 9 spots in middorsal rows from nape to base of tail, spots from 10 to 12 mm long, from 8 to 10 wide, and involving from 12 to 16 rows of dorsal scales; lateral spots smaller; transverse bars not distinct, confused with light areas surrounding the enlarged spots; gular region marked with several parallel dark, longitudinal stripes extending from labials to posterior edge of ear, a few spots between median strip and first lateral strips; legs marked with large spots; body ground color cream to light gray.

RANGE.—Lahontan Basin in western Nevada northwest into northeast California, north into southern Oregon, and northeast into the Snake River Valley of southwestern Idaho.

Crotaphytus wislizeni wislizeni
Baird and Girard

SPECIMENS EXAMINED.—Arizona, Yuma Co., CAS 33486, 34204-8 and 33490; SDNHM 16730 and 17123; MMZ 71080(4) and 71080(2). California, Imperial Co., BYU 41177; LACM 4007, 15649, and 37787-8; LBSC 1471-2; MMZ 122632(2); SDNHM 1879, 7143, 7847, 10937, 11346, 13352, 13911, 18596, 20967, 28762, 36541, and 39735. Inyo Co., CAS 65117, 65318-20, 65336, 65381, 65486-8, 65529-31, 65583-4, and 65634; LACM 26804-6, 36668-9, and 52876; SDNHM 2503 and 12243. Kern Co., CAS 21234; LACM 4013, 26803, 53883-4, 63807, 63809-10, and 94709; MVZ 26026 and 70372; SDNHM 5877, 6047, 15877, 19483-5, 37438, 40005, and 41803. Los Angeles Co., LACM 4009, 15628-30, 15631, 15632-33, 15634, 15635, 15636, 15637, 15638, 15639, 15640, 15641-2, 15643, 15644, 15645, 15646-7, 15710, 26802, 52878, and 52879; MVZ 873 and 19652-4. Mono Co., SDNHM 28941. Riverside Co.,

BYU 40941-3 and 40945; CAS 45369-70; LACM 4011, 15648, 22218-9, 26807-8, and 52880-82; SDNHM 4999-5000, 8040, 11344, 19486, 20700-3, 22352, 29448, 31428, 31906-7, 39747, 39850, and 41339. San Bernardino Co., BYU 3108 and 40942; CAS 43181-4; LACM 4012, 4014, 15653-61, 21646-49, and 52877; SDNHM 2489, 2498, 4408, 5875-6, 7798, 9013-5, 20887, 23636, 25344, 25641-2, 28939-40, 28942, 29660, 31453, 38889, and 41201. San Diego Co., LBSC 1473-4; LACM 15651-2; SDNHM 44, 8041, 9952, 11099, 11345, 18593-5, 22328, 23411, 24036, 29516, 33943, and 38418.

Nevada, Clark Co., BYU 460, 504, 556, and 1541-2; LACM 15681-95; MMZ 84941(2), 90699-01; SDNHM 7626-7, 31718, 38675, and 40655-7. Elko Co., CAS 40933. Esmeralda Co., CAS 37801. Lander Co., BYU 2918; MMZ 84945 and 91868. Lincoln Co., BYU 9816; CAS 37014-18 and 38019-23. Mineral Co., MMZ 84948 and 117360. Nye Co., BYU (Nevada Test Site including Mercury and Rock valleys and areas in and associated with Frenchman, Jackass, and Yucca Flats) 3037-51, 5084-7, 3093-98, 17276-9, 17308-22, 17944, 18969, 18984, 21740-55, 23620, 23966, 30083, 30085-7, 30121, 30539, 30546, 30589-90, 30595, 30608-9, 31425, 31810-14, 32571, 32632-4, 33571, 33609, 40127, and 41452-5; CAS 37017-8, 37512-3, 37688-92, 37996, and 38019-23; LACM 15696 and 26810; MMZ 84942(2), 34943(4), 34946, 84951, 84953-6, 84957(2), and 117336. White Pine Co., BYU 558.

Utah, Beaver Co., BYU 580, 4302, 11349-53, and 12001-2. Iron Co., BYU 478, 2371, 2374, 2376-7, and 2899; MMZ 59573, UU 1659. Juab Co., BYU 2731, 3020, 3027, 10244, 11295-6, and 12496; MMZ 91870(2). Millard Co., BYU 481, 580, 4308, 9099, 10179, 11354, and 14843-53; CAS 893-4, 1530-2, 38031, 85399-00, and 54151-2; MMZ 70553, 70554(6), 70555(14), 70556(2), 70557(2), 70558-60, 70561(2), 60562-3, 70564(3), 70565(4), 70566, 70567(5), 70568(2), 70569(3), 70570(3), 84950, and 91869; SDNHM 893-4, 1530-2, and 26399-02. UU 3298-01. Salt Lake Co., UU 18. Sevier Co., SDNHM 37960, 38315-6, 38244-50, 38328-31, 38381-2, 39016-8, 39191,

39397-9, and 40571-3. Tooele Co., BYU 480, 1555, 14688, and 14843-53; MMZ 69432(2), 69433-4, 69435(4), 69436-7, and 91823; SDNHM 22998, 24988-9, and 26399-402. Utah Co., BYU 483, 576, 1578, 1633, 2210-11, 8496, 12196, 14690-1, 16601, 21506, 22474, and 22835; UU 1-4, 2a, and 3563-7. Washington Co., BYU 515, 680, 1635, 8464, 11382, 23657, 31970-1, and 31972-8; CAS 54085-6; SDNHM 21078, 24993, and 25643.

Mexico: Baja California Norte, BYU 23336; CAS 57446 and 90256; Sonora, BYU 3175; CAS-SU 17049-50; SDNHM 38251-4, 38605-6, 38888, and 40601; USNM 146455.

Crotaphytus wislizeni maculosus
subsp. nov.

SPECIMENS EXAMINED.—California, Modoc Co., CAS 63912; LACM 4010. Idaho, Ada Co., CAS 41366-71, 45417-25, and 53781-3. Boise Co., MMZ 54072, 68245(2), 68246-8, and 93084(4). Bingham Co., CAS 41275-6. Butte Co., BYU 30773. Canyon Co., MMZ 68249. Elmore Co., MMZ 60250; SDNHM 1452. Owyhee Co., BYU 2835; CAS 55261, 64151-4, and 64161-2; MMZ 68251(2), 122787(2), 122790, and 125694.

Oregon, Harney Co., BYU 41445, 41454-71; Malheur Co., MMZ 124618(2).

Nevada, Churchill Co., MMZ 72653, 84944(2), and 84949; Humboldt Co., MMZ 43171-7, 60029, 77996, 85618(5), and 91865-7. Lyon Co., LACM 15696. Ormsby Co., SDNHM 38417. Pershing Co., MMZ 84947 and 91825(2). Washoe Co., CAS 38016-7, 40510-15, and 40527-32; MMZ 91824, 91826(2), 91827(2), and 91828-9.

Crotaphytus wislizeni silus
Stejneger

SPECIMENS EXAMINED.—Fresno Co., CAS 22713, 22716-8, 22857-8, 23212-3, 23250, 23271, 23292, and 85416; King Co., MVZ 116442; Kern Co., CAS 3046, 39000, 43266, and 47996; LACM 4008, 15662-9, 15671-6, 15679-80, and 26809; San Luis Obispo Co., CAS 32195, 23200, and 23203-4; MVZ 2751, 8817, and 61077. MVZ 2725, 2733, 2735, 2737-43, 2747, 2749, 3775-81, 4891-2, 4894-8, 6851, 43142, and 72353-4.

Specimens showing one or more inter-

grading characters with *C. w. wislizeni*: CAS 1243, 12787-8 (Frazier Park), 38999 (Tehachapi Mts.); LACM 15650 (Mt. Pinus), 15670 (25 mi S. Bakersfield), 15671 (Wheeler Ridge), 15677 (McKittrick), 52879 (Black Butte), 15630-3 (Lovejoy Sp.), 15635 (Piute Butte); MVZ 43139 (3 mi SW Kicks Corner).

MORPHOLOGY AND VARIATIONS

These attractive lizards of moderate size have only recently been critically examined. Since Smith (1946) noted the considerable variation in patterns, we have observed a correlation between color patterns and geographic distribution. Tanner and Banta (1963) described and figured the pattern for *C. w. wislizeni* in Arizona and New Mexico and for *C. w. punctatus* in the upper Colo-

rado River Basin. Montanucci (1970) discussed in detail the color patterns of *C. w. silus* in the San Joaquin Valley of California. Although these and other studies have made some comparisons with those populations occurring in the Great Basin, a critical examination of a large series has not been made. It is hoped that this study will yield the results necessary to provide some conclusions for the leopard lizards of this large and varied area.

COLOR PATTERN TYPES

SPOTTING.—In the western United States and northern Mexico there are five distinct spotting patterns:

1. A pattern of moderately sized spots, with a circle of light spots surrounding the larger dark spots. This pattern is prominent

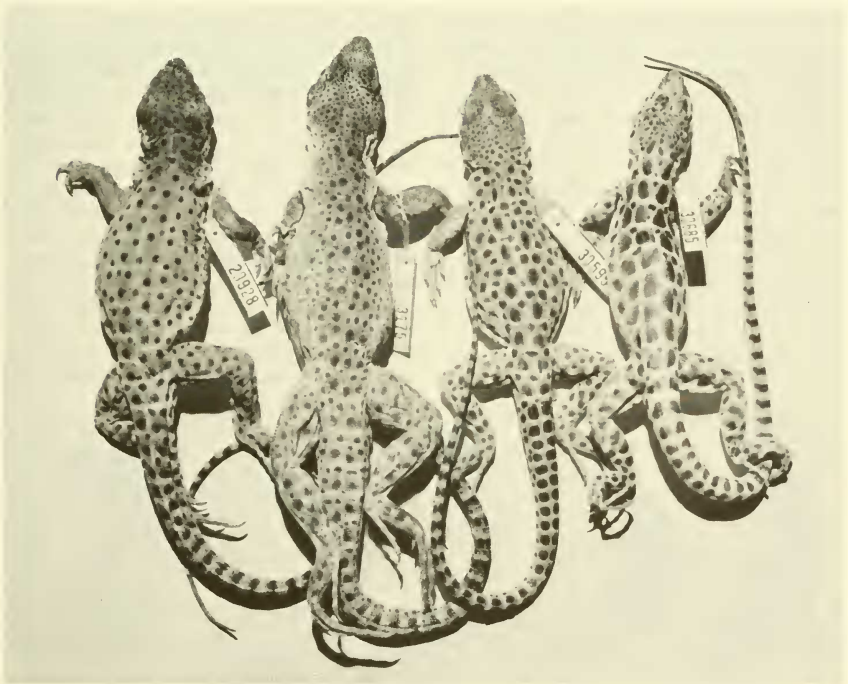


Fig. 4. Dorsal views of (a) *C. w. punctatus*, (b) *C. w. wislizeni*, (c) *C. w. wislizeni* NTS intergrade, (d) *C. w. maculosus*.

on the dorsal aspect of the trunk, base of the tail, and hind legs. There may also be smaller spots interspersed between the larger ones and on the lateral parts of the trunk and tail. The white transverse bars may or may not be apparent; when present they are more obvious posteriorly on the trunk and base of tail (Fig. 4b).

2. A pattern of small spots, widely dispersed on the trunk, tail, and legs. The background is lighter than in those with other patterns. Individuals with this pattern show no white dots in association with the small dark spots. Furthermore, there is a greater uniformity in the size of spots than in other patterns. The white bars are distinct but narrow and less prominent than in populations occurring west of the Colorado River (Fig. 4a).

3. A pattern of moderate to large spots, with light centers in juveniles but not in adults. The light center is apparently lost by a gradual darkening and blending with the ground color. As the blending of colors occurs, the spots are subdivided to form from two to four closely associated or slightly connected spots. This pattern is characteristic of *C. w. neseotes* from Cedros Island and many individuals from Baja California, Mexico.

4. A pattern in which the areas between the white transverse bars are from a solid dark brown to a nearly black color. In juveniles there are spots present, but these are lost in adults by a suffusion of dark pigment that obscures all spotting. The transverse white bars are distinct and much wider than

in other patterns. This pattern occurs in the populations in the lower parts of the San Joaquin Valley. We note, however, that the spotted pattern of juvenile *C. w. silus* is very similar to that of adults from Antelope Valley (Fig. 5).

5. The subspecies *C. w. maculosus* has a pattern of large dark spots between the transverse white bars and a lighter continuous cycle around the larger spots. This is reminiscent of the pattern in *C. w. wislizeni* except for larger spots and a light circle rather than a series of small light spots. The transverse white bars are moderate in size, being narrower than in *C. w. silus* but wider than in *C. w. punctatus*. In some individuals the transverse bars become diffused and blended with the light circles, which produces an irregular netlike configuration of light markings (Fig. 4d).

Montanucci (1970) referred to those light dots, circles, and other additions to the spotted pattern as adornments. This is seemingly an appropriate way to treat all additions to the basic pattern of spots. Only a few populations are without adornments. Specimens of *C. w. punctatus* from southeastern Utah have a light ground color and small dark brown spots (Tanner and Banta 1963). Those from near Bakersfield, Kern County, and north in Fresno County, California, have as adults reduced the pattern to a uniform dark color between the light transverse bars, thus eliminating the basic spot pattern.

An examination of hatchlings and small juveniles demonstrates that *C. wislizeni* has



Fig. 5. Dorsal view of specimens of *C. w. silus* (A-C; D and E, intergrades, Antelope Valley). LACM tags.

throughout its wide range maintained a spotted pattern in its young. This juvenile pattern is modified in adults of all color pattern types. The similarity of hatchling patterns is unique, and we are impressed with this unifying character throughout the species. Adjacent populations with very different adult patterns such as Antelope Valley (Los Angeles County), with its spotted pattern and the dark nonspotted pattern in the Bakersfield population (Kern County), have similar spotted patterns in hatchlings and young juveniles. Populations occurring between those populations with patterns as described above (1-5) show many variants. This is most evident in populations occurring in southern Nevada, in which a series from valleys such as Frenchman Flat or Mercury may have individuals with patterns similar to all other populations except that pattern found in the San Joaquin Valley (Fig. 2). In patterns 3 and 5 the white transverse bars may be absent on all or part of the trunk or so intertwined with the light areas between the spots as to lose their identity.

SCALE PATTERNS

POSTMENTALS.—Only a few scale patterns vary noticeably within this species. As noted in Part I (Tanner and Banta 1963), the postmentals show significant variations between *C. w. wislizeni* and *C. w. punctatus*. We have reexamined this character in 101 specimens from the Upper Colorado River area of southeastern Utah and northeastern Arizona, and our findings indicate an average postmental count of 5.71 in con-

trast to the 5.72 reported by us in 1963 (Table 1). This figure includes a series from Kane County, Utah, which has a lower average (5.17), and we consider Kane County to be a lane of dispersal into southwestern Utah and eastern Nevada. If the specimens from Kane County are removed, the postmentals for *C. w. punctatus* average 5.81.

In Table 2 we have averaged the postmentals for Washington County, and for populations in the Great Basin of west central Utah, Nevada, California, Oregon, and in the Snake River Valley of southwestern Idaho. These figures show an average decrease in the numbers of postmentals from east to west. However, this decrease is accompanied by an increase in the range of variation. We consider this a strong indicator of intergradation, particularly in those populations occurring in Washington County, Utah, the Great Basin of west central Utah, at the Nevada Test Site, and in southern Nevada.

Those populations occurring along the northern limits of distribution (Table 2: Harney County, Oregon, and southwestern Idaho) show a noticeable increase in the number of postmentals when compared to other Great Basin populations. These same populations also show a decrease in the range of variation, with none of the Oregon

TABLE 2. Variation in the postmentals in the Great Basin and adjacent areas in Utah, Nevada, Oregon, Idaho, and California.

Area	Number	Range	Mean
Washington County, Utah	15	4-5	4.5
Great Basin			
Western Utah	57	2-6	4.1
Nevada Test Site	56	2-7	4.2
Lahontan Basin	29	2-6	4.1
Harney County, Oregon	9	4-6	5.0
San Bernardino, Riverside County	77	2-6	4.2
Inyo County	23	2-6	4.4
Imperial County	21	3-6	4.4
Antelope Valley, Los Angeles County	31	2-6	4.4
Snake River Valley			
Southwest Idaho	34	3-6	4.6
	352		

TABLE 1. Variation in the postmentals in populations occurring in northern Arizona and southeastern Utah.

Area	Number	Range	Mean
Utah Populations			
Grand County	34	4-7	5.7
Emery County	17	5-7	6.0
Garfield County	15	4-7	5.9
San Juan County	6	4-6	5.5
Northeast Arizona	6	4-7	5.8
Kane County	23	4-6	5.2
	101		5.71

specimens with less than four and only one Idaho specimen with three postmentals. Although our samples are small for some populations (Oregon), they show consistency except for Washington County, Utah, which we include with the large and varied intergrading populations occurring in southwestern Utah and much of central and southern Nevada. The increase in the number of postmentals for the northern populations of the subspecies *maculosus*, and for that matter *punctatus*, is not explainable except as a response to the climatic changes in the northern localities.

An examination of the scale pattern summaries in Table 3 indicates that there are only minor variations. A few trends are apparent, such as a higher range and average for femoral pores and the scale rows around the body in the populations of Baja California Sur, Mexico. In neither of these patterns does the lower limits of the range show as few pores or rows of scales as in other populations. Only in the higher averages, particularly in the scale rows, are the variations between the Baja California Sur and the continental populations obvious. In all populations and subspecies there is an overlapping in the ranges of all scale patterns

examined. In most patterns this overlapping is extensive.

The Nevada Test Site population shows greater variation than other adjoining populations in the number of scale rows, ventrals, and postmentals. In the scale rows the average is low, with only *C. w. punctatus* lower. The ventrals average the lowest of all populations studied, and the range for the postmentals from two to seven is greater than in other populations.

SKULL MEASUREMENTS

SKULL LENGTH/WIDTH RATIO.—The ratio of the skull width into its length (Fig. 6) substantiates the data presented by Montanucci (1970) that the skull is shorter in the San Joaquin population (*silus*) than other subspecies and populations. There is, however, an overlapping with other populations of approximately 25 to 50 percent when compared with other populations examined (Fig. 6).

DISCUSSION

On the basis of color and color pattern, we must assume that *C. wislizeni* expanded

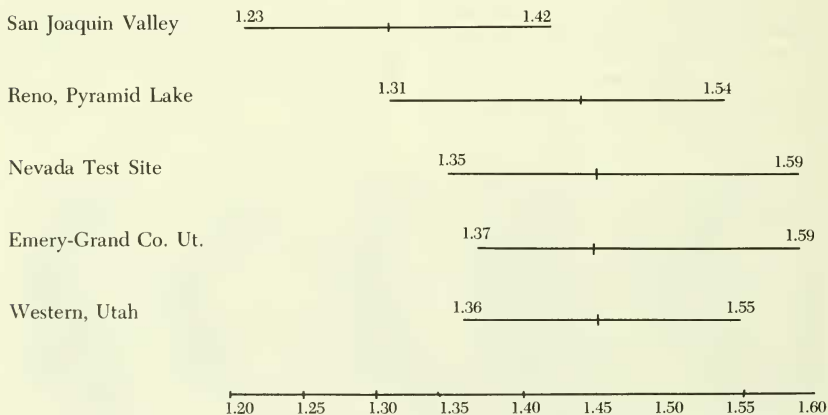


Fig. 6. Ratio of width into skull length (from rostral to median posterior of skull). Specimens used and data available on request.

TABLE 3. Scale patterns in subspecies or populations of *Crotaphytus wislizeni* (mean in parenthesis).

Subspecies or population	Total femoral pores	Total supralabials	Total infralabials	Scale rows	Dorsals	Ventrals	Post-mentals
<i>C. w. mesoetes</i>	37-59(45.9)	26-32(27.9)	24-30(27.4)	♂ 186-202(193.5) ♀ 185-207(199.7)	180-206(194.5) 191-208(200.6)	86-101(92.4) 91-105(96.6)	2-4(3.6)
<i>C. w. copei</i>	38-54(46.2)	27-32(29.5)	26-33(29.9)	184-212(196.4)	175-227(200.7)	86-110(95.6)	2-6(4.0)
<i>C. w. wislizeni</i>							
1. Arizona, New Mexico, Texas, Chihuahua, and Sonora	34-50(42.1)	24-34(28.8)	24-33(28.3)	176-200(183)	174-231(205.6)	95-112(106.2)	2-6(3.7)
2. S. Nevada and S. California	36-55(43.8)	26-37(30.8)	24-35(29.6)	164-214(191.2)	170-245(213.1)	85-118(101.0)	2-6(4.3)
3. SW. Utah, Great Basin and E. Nevada	31-47(38.0)	22-37(28.4)	21-30(25.4)	154-190(182.0)	180-217(196.5)	84-116(96.0)	2-6(4.0)
4. Nevada	35-45(39.9)	24-36(30.0)	22-33(27.5)	148-198(171.8)	172-210(194.0)	72-102(87.1)	2-7(4.1)
<i>C. w. maculosus</i>	34-47(39.95)	25-39(30.1)	25-34(29.2)	165-192(179.0)	175-212(193.4)	87-114(95.7)	3-6(4.45)
<i>C. w. punctatus</i>	35-52(42.35)	25-36(29.6)	24-35(29.1)	145-181(164.7)	178-215(199.2)	85-121(101.2)	4-7(5.7)

its range rapidly at the close of the Pleistocene and occupied the low valleys in southern New Mexico, southern Arizona, northern Sonora, and southern California, perhaps before entering the areas of the high plateaus. Such an hypothesis would have much of southern California, southern Nevada, and the low valleys along the California-Nevada line occupied before the invasion of *C. w. punctatus* occurred in western Utah and east central Nevada. This hypothesis is based on the fact that color patterns in southern California, the Antelope and San Joaquin valleys of California, and the populations in northern Nevada (*maculosus*) do not seem to be in any way similar or related to the *punctatus* pattern. The invasion of western Utah and southeastern Nevada by *punctatus* seems to have occurred more recently. This is based on the fact that there is a real jumbling of patterns in southern Nevada (NTS); and from this general area a diminishing effect is seen as one examines specimens from the southwest and north. To the northeast, that is from southern Nevada to Washington County, Utah, the influence of *punctatus* increases. If populations of *wislizeni* had occupied these areas before *punctatus* arrived, they have or are in the process of a continuing and extensive introgression with a strong *punctatus* influence. This is most obvious throughout southern and extreme eastern Nevada.

There is reason to suspect that the main flow of leopard lizard migration at the close of the Pleistocene was from southern California, through the low valleys of eastern California north into the Lahontan Basin of west central Nevada. As the higher valleys of western Utah and eastern Nevada became environmentally available, they were occupied. Furthermore, with improving climatic conditions, the terrain (with its north-south-oriented mountains) is well suited for a rapid movement to the north (or south) through the broad alluvial valleys.

Migration into the Bonneville Basin of western Utah and the high valleys of central and eastern Nevada was slower. Elevation barriers ranging up to 5,000 feet may have remained cool and were probably

most responsible for slowing the northward movement. This is still effective for some species such as *Sceloporus magister* and *Callisaurus ventralis*, which are not in the Bonneville Basin but have reached the Lahontan Basin. The early arrival and partial isolation in the Lahontan Basin provided a greater opportunity for differentiation and also time to extend their ranges into southern Oregon, northeastern California, and southwestern Idaho. Although those populations now in the Bonneville Basin are partially isolated, they appear to have been derived too soon to have differentiated as much as those occupying the Lahontan Basin.

In western Utah, southern Nevada, and adjoining California (San Bernardino and Inyo counties) there is a large area of intergradation between those populations existing in the area or those that moved north from southern California (*C. w. wislizeni*) and those moving into the area from southeastern Utah and northern Arizona (*C. w. punctatus*). Because of the size of the area of intergradation, one may assume that the gene flow from these populations has been strong and steady. As one samples populations radiating from this central area, the populations are more homogeneous. The one area of intergradation most difficult to interpret is the populations in the Bonneville Basin of western Utah and eastern Nevada. Within this basin (from Iron County to Box Elder County, Utah) the populations are more homologous than those from the Nevada Test Site, but they still provide an occasional individual with either a *wislizeni* or a *punctatus* pattern.

Apparently, introgression had occurred before the Bonneville Basin was occupied, or there was a mingling of the two as they moved northward at about the same time. Once movement was slowed and population stability was achieved, differentiation occurred. This is seen in such populations as those in the Lahontan Basin and San Joaquin Valley, and to an extent in Antelope Valley (Los Angeles County) and the Coachella Valley. Differentiation has occurred primarily on the fringes of distribution, with the large central area in southwestern Utah,

southern Nevada, and much of southeastern California occupied by a population with variable degrees of intergrading characteristics.

Perhaps the most difficult populations to understand occur in the areas of western San Bernardino County (west of Barstow), eastern Kern County (near Mojave), and northern Los Angeles County (Palmdale-Lancaster area). Populations in these areas are far enough removed from the intergrading population of southern Nevada to reflect some pattern characteristics of their own. This is particularly true for Antelope Valley in northern Los Angeles County, where a darker ground color obtains and the spots are darker and more uniform in size and color. Although our samples are small, those seen reflect a slow but steady change from *C. w. wislizenii* to *C. w. silus* from western San Bernardino County through Antelope Valley to the areas near Fraser Park and on westward into the low hills and valleys of northern Ventura and Santa Barbara counties.

The data concerning *C. w. silus* presented by Montanucci (1970) agrees generally with our findings. Any differences are in the area of interpretation. We see in adjoining populations (Antelope Valley, Los Angeles County, and those near Weldon, San Bernardino County) strong influences of the adult and juvenile color patterns of *C. w. silus*. We also recognize a more sudden change in pattern from the foothills surrounding the San Joaquin Valley to the valley floor.

In other areas of the extensive leopard lizard range ecological changes are more gradual, or they occur in smaller geographical areas which do not seemingly provide sufficient space for isolation and thus slowly induce genetic adaptive change. This gradual change in the environment has provided for wide areas of introgression in much of the Great Basin and is perhaps unique in that the central area of distribution (southern and eastern Nevada, southern California, and western Utah) represents a large area of genetic variation as deduced from the phenotype. As indicated above, within this wide area of diversity subspecific patterns (except for *silus*, *copei*, and *nescotes*)

appear in some individuals. Within the populations considerable individual variation occurs and is so extensive in some areas that few lizards show the same phenotypic pattern. Only in the fringe areas where some degree of isolation obtains do we find subspecies or incipient subspecies.

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